

Pteronotus parnellii. By Robert M. Herd

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Pteronotus Gray, 1838

Pteronotus Gray, 1838:500. Type species *Pteronotus davii* Gray, 1838, by original designation.

Chilonycteris Gray, 1839. Type species.

Chilonycteris macleayi Gray, 1839, by original designation.

Lobostoma Gundlach, 1840. Type species presumably *Lobostoma quadridens* Gundlach, 1840, by original designation, = *Chilonycteris macleayi* Gray.

Phyllodia Gray, 1843. Type species *Phyllodia parnellii* Gray, 1843, by original designation.

Dermonotus Gill, 1901. Replacement name for *Pteronotus* Gray, 1838.

CONTEXT AND CONTENT. Order Chiroptera, Suborder Microchiroptera, Family Mormoopidae. *Pteronotus* contains six living species in three subgenera (following key adapted from Smith, 1972:55).

- 1 Wing membrane fused on middorsal line giving a naked-back appearance; rostral breadth always greater than length of maxillary toothrow (*Pteronotus*) 2
Wing membrane not fused on mid-dorsal line; rostral breadth equal to or less than length of maxillary toothrow 3
- 2 (1) Wing membranes sparsely covered by long, irregularly-spaced hair; length of forearm less than 50 mm *P. davii*
Wing membranes covered with many short hairs, giving the back a "velvety" appearance; length of forearm usually equal to or greater than 50 mm ... *P. suapurensis*
- 3 (1) Basioccipital narrowly constricted between auditory bullae; basisphenoid with two narrow and deep furrows; length of forearm usually more than 50 mm (*Phyllodia*) *P. parnellii*
Basioccipital not narrowly constricted between auditory bullae; furrows in basisphenoid wide and shallow; length of forearm usually less than 50 mm (*Chilonycteris*) 4
- 4 (3) Wing membranes and uropatagium attached to ankle by way of a short ligament that is tightly bound to tibia; infraorbital foramen opening just slightly anterior to maxillary root of zygomatic arch, canal formed by a thin spicule of bone *P. personatus*
Wing membrane and uropatagium attached to ankle by way of a long ligament that is tightly bound to the distal half of the tibia; infraorbital canal opens at the end of a short tubular canal. 5
- 5 (4) Labio-nasal plate with a squared lappet above each nostril; length of forearm usually more than 40 mm *P. macleayi*
Labio-nasal plate with three to four wart-like tubercles above each nostril; length of forearm usually less than 40 mm *P. fuliginosus*

Pteronotus parnellii (Gray, 1843)

Parnell's Mustached Bat

Phyllodia Parnellii Gray, 1843:50. Type locality unspecified in Jamaica.

Chilonycteris rubiginosus Wagner, 1843:367. Type locality Cai-cara, Mato Grosso, Brazil, by revisor's designation (Smith, 1972).

Chilonycteris osburni Tomes, 1861:66. Type locality Sportsman Hall and Oxford Cave, Manchester, Jamaica.

Chilonycteris boothi Gundlach, 1861:154. Type locality "in Fundador, auch in Guines", [Matanzaz and Habana provinces, Cuba] by revisor's designation (Smith, 1972).

Chilonycteris mexicana Miller, 1902:401. Type locality San Blas, Tepic, Mexico.

Chilonycteris portoricensis Miller, 1902:400. Type locality near Pueblo Viejo [Cueva di Fari], Puerto Rico.

CONTEXT AND CONTENT. Context noted in generic summary above. The nine recognized subspecies are:

P. p. fuscus (Allen, 1911:262). Type locality Las Quiguas, 5 mi south of Puerto Cabello, Venezuela.

P. p. gonavensis (Koopman, 1955:110). Type locality near En Cafe, La Gonave Island, Republic of Haiti, Hispaniola.

P. p. mesoamericanus Smith, 1972:71. Type locality 1 mi south and 0.75 mi east Yepocapa, Chimaltenango, Guatemala.

P. p. mexicanus (Miller, 1902:401), see above.

P. p. paraguayensis Linares and Ojasti, 1974:74. Type locality "cueva de Piedra Honda ... 7 km al SW de Pueblo Nuevo, 120 m de altura, Peninsula de Paraguana, Estado Falcon, Venezuela."

P. p. parnellii (Gray, 1843:50), see above (*osburni* Tomes and *boothi* Gundlach are synonyms).

P. p. portoricensis (Miller, 1902:400), see above.

P. p. pusillus (Allen, 1917:168). Type locality Arroyo Salado, Santa Domingo.

P. p. rubiginosus (Wagner, 1843:369), see above.

DIAGNOSIS. A mormoopid bat (Fig. 1) differing from *Mormoops* in having relatively primitive conditions for some characters, tragus not so ornamented, rostrum only slightly elevated, more or less on same plane as braincase, braincase large, ears with lanceolate tips. Diagnostic features of *Pteronotus parnellii* within the genus are included in the key above.

GENERAL CHARACTERS. Males average slightly larger than females, this difference becoming progressively greater southwardly in their range. Size differences are most apparent in cranial dimensions. Geographic variation is apparent in both sexes; there is a general increase in external and cranial size, along with a less marked change in color from pale to dark, at progressively more southern latitudes (Smith, 1972). The ranges in measurements (in mm) for selected characters are: length of forearm, 50 to 65; total length, 73 to 102; length of tail vertebrae, 18 to 28; length of hindfoot, 12 to 17; length of ear from notch, 18 to 28; zygomatic breadth, 10.0 to 13.4; rostral breadth, 6.4 to 8.8; length of maxillary toothrow, 7.3 to 9.9; condylobasal length, 17.0 to 21.9; depth of cranium, 7.9 to 10.0 (Smith, 1972); and body weight, 10 to 20 g (Walker et al., 1975). The annual molt (May to July) accounts for the different color phases reported by early collectors, and was described by Smith (1972). Fresh pelege is usually dark Prouts Brown or blackish; as it ages it becomes paler (Snuff Brown) or may



FIGURE 1. *Pteronotus parnellii* in flight. Photograph by Tim Strickler.

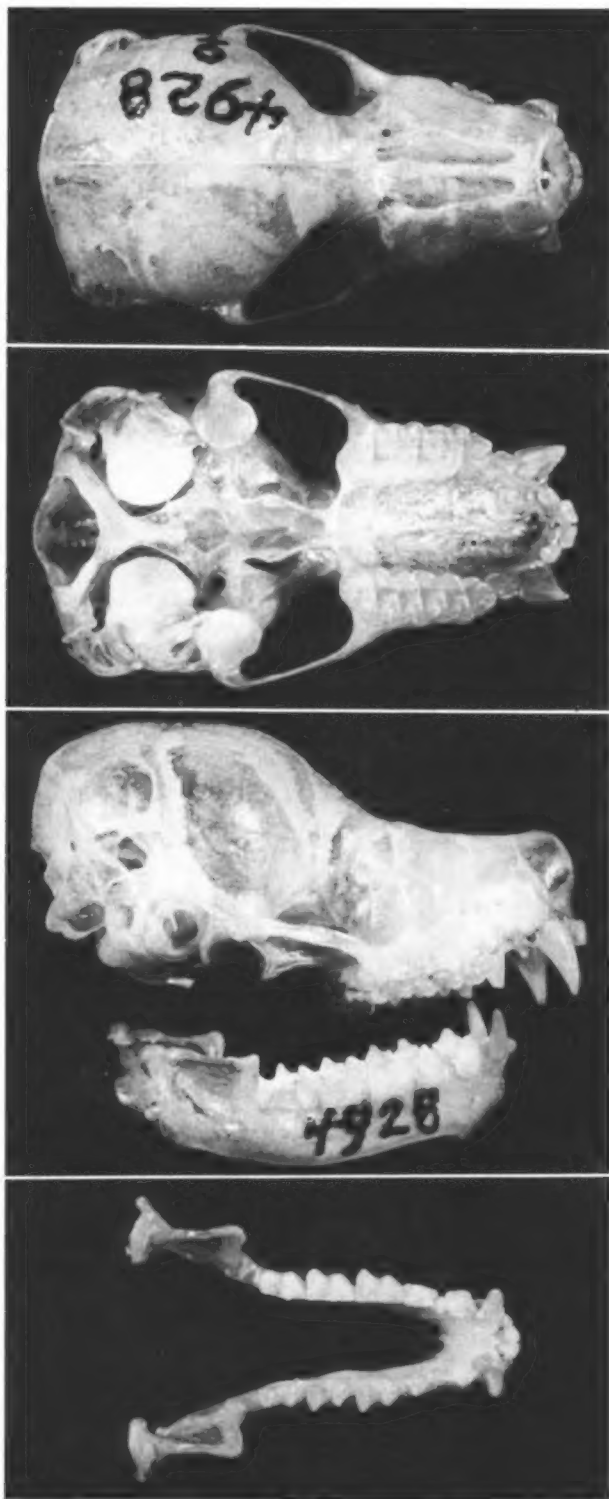


FIGURE 2. The skull of a female of *Pteronotus parnellii rubiginosus* from Barro Colorado Island, Canal Zone, Panama (Carleton Univ., Dept. of Zoology, no. 4928). Condylobasal length 21.5 mm. Photographs by author.

progress to a brilliant fulvous or orange. The profile of the skull (Fig. 2) is relatively flat, the rostrum is not elevated, and the forehead slopes gradually onto the rather long, broad braincase. The upper incisors are robust and peg-like, the inner pair distinctly bifurcate and with broad, rounded heels; the lower incisors are also heavily constructed, the inner pair trilobed, the outer pair bilobed (Smith, 1972).

DISTRIBUTION. Parnell's mustached bats are found on the Greater Antilles and the mainland from southern Sonora and

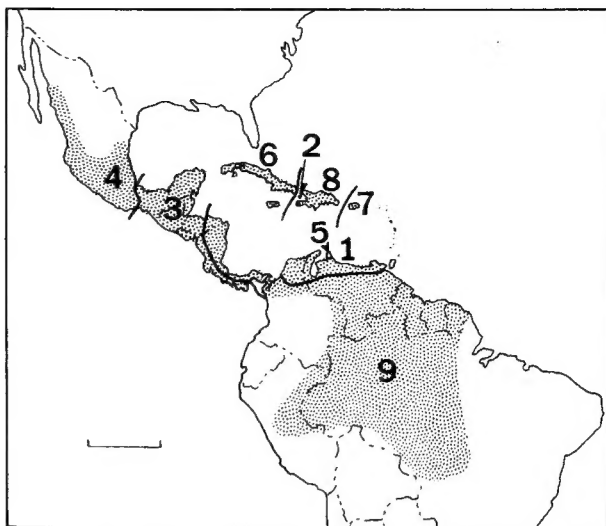


FIGURE 3. The distribution of *Pteronotus parnellii* and its subspecies based on Smith (1972): 1, *P. p. fuscus*; 2, *P. p. gonavensis*; 3, *P. p. mesoamericanus*; 4, *P. p. mexicanus*; 5, *P. p. paraguayensis*; 6, *P. p. parnellii*; 7, *P. p. portoricensis*; 8, *P. p. pusillus*; and 9, *P. p. rubiginosus*.

Tamaulipas, Mexico, southward along Pacific and Gulf coastal lowlands, throughout Central America, and into South America, where they occur along the Caribbean coast (including Trinidad) and south into the Amazon Basin to the Mato Grosso region of Brazil (Smith, 1972). These bats have not been reported from west of the Andes in Colombia, Ecuador, or Peru, nor from Bolivia, French Guiana, or eastern Brazil (Smith, 1972). The ranges of the subspecies are shown in Fig. 3. The limited fossil record consists of late Pleistocene remains in Puerto Rico and sub-Recent cave deposits in Jamaica, Cuba, and Mexico (Martin, 1972).

FORM AND FUNCTION. The prominent facial features of *P. parnellii* are the apparently naked outgrowth or "chin-plate," and the anteriorly directed tufts of long hairs on the sides of the muzzle from which the common name, mustached bat, is derived. The facial glands of *P. parnellii* are similar to those of other mormoopids (Dalquest and Werner, 1954). The tragus has a simple lanceolate shape with a secondary fold of skin that forms a small pocket-like structure in the cranial edge (Smith, 1972). The dental formula is $i\ 2/2$, $c\ 1/1$, $p\ 2/3$, $m\ 3/3$, total 34 (Phillips and Jones, 1968). The teeth of 292 specimens of *P. parnellii* contained four incidences of developmental abnormalities and five cases of disease or mechanical damage (Phillips and Jones, 1968).

The head of the humerus is ovoid and the supraglenoid fossa is well developed. Together these may limit rotation at the shoulder joint during flight, and compensate *P. parnellii*, and the other mormoopids, for the lack of a "locking" device, such as the double articulation between the humerus and scapula of phyllostomids (Smith, 1972). The pectoral (downstroke) muscles of *P. parnellii* contain three main fibre types (fast-twitch glycolytic, fast-twitch oxidative-glycolytic, and slow-twitch oxidative). Possession of all three types may allow *P. parnellii* a diversity of muscle function and flexibility in its flight behavior (Strickler, 1980). The morphology of the forelimb of *P. parnellii* was described in detail by Vaughan and Bateman (1970) and Smith (1972). Associated with its rapid, enduring flight, there has been a trend toward the reduction of the weight of its wing. Reduction was accomplished by: specializations in the muscle attachments; simplification of the musculature; reduction in the elasticity of major extensors and flexors of the digits; and specializations of the elbow joint and the distal end of humerus. Flexion of the distal part of the wing of *P. parnellii* is controlled by an automatic flexing device formed by the distal spinous process of the distal end of the humerus and the muscle, *M. flexor carpi ulnaris*. This automatic flexing device contributes to the more specialized mode of flight of mormoopids as compared to the rather generalized flight of the closely related phyllostomids in which wing flexion is controlled solely by muscular effort (Smith, 1972). The wings of *P. parnellii* are relatively long, and have an above-average (of all bats) wing aspect ratio. They are less specialized than those of other mormoopids (Smith and Starrett, 1979).



FIGURE 4. Sonograms of three orientation pulses of *Pteronotus parnellii parnellii* (redrawn from Pollak and Henson, 1973, by permission of G. Pollak and Springer-Verlag New York, Inc.). The record for each pulse shows the long CF component, the initial and terminal FM components, and the harmonic series. The three components of the second harmonic are the most intense as indicated by the darker trace.

The central nervous system of *P. parnellii*, although displaying many basic mammalian features, contains several features shared by other microchiropterans. It was described in detail by Henson (1970). The microchiropteran spinal cord is one of the shortest known amongst mammals. In *P. parnellii* it terminates at about the level of the twelfth thoracic vertebra. The cervical region is enlarged, as are the spinal ganglia of the cervical roots, and together with its short length, reflect the well-developed upper extremities of bats. The *substantia gelatinosa*, which is thought to exert a regulatory influence on other dorsal horn neurons, is remarkably well developed, and this is particularly apparent in cross-sections of the lower segments of the spinal cord. The vomeronasal organ of *P. parnellii* is moderately developed and extends into the nasal septum beyond the vomeronasal cartilage, yet the nasopalatine duct is entirely lacking (Bhatnagar, 1980).

The stomach of *P. parnellii* is simple in overall configuration, having a thick and asymmetric pyloric sphincter and small fundic caecum, and has an extensive complement of zymogenic cells. It is similar to stomachs of North American bats of the family Vespertilionidae (Forman, 1971). In common with other insectivorous bats, *P. parnellii* has a restricted distribution of Peyer's patches in its intestine: one to three patches being observed in the proximal half of its intestine. These lymphoid tissues have a possible role in immunologic responses.

ONTOGENY AND REPRODUCTION. *Pteronotus parnellii* follows a pattern of seasonal monestry (Wilson, 1973). Copulation occurs in January, followed by gestation and parturition in May. Lactation may continue till the end of July. Parturition coincides with the annual insect bloom at the onset of the rainy season. The young are born morphologically immature and are helpless at birth; they are relatively immobile; eyes are closed and skin is naked. Their auditory responsiveness is the most developed of any infant bat studied but their audiogram lacks the sharp tuning present in the adult (see BEHAVIOR; Brown and Grinnell, 1980).

ECOLOGY. *Pteronotus parnellii* has rather broad habitat associations, occurring in humid to arid habitats from coastal lowlands to 3,000 m (Smith, 1972). It is a common bat throughout its range, roosting during the day in caves and mines, which it often shares with other species of bats. Parnell's mustached bat prefers to roost in the largest chambers of large, humid caves. It emerges shortly after sunset and remains active for 5 to 7 h. In January a sex ratio of 1:1 of individuals sharing roosts, and frequent visits to the roost during the evening, are coincident with the period of copulation and may represent "swarming" (Goodwin, 1970). Following this period the sexes appear to segregate at different roosts.

Pteronotus parnellii does not use night roosts and is assumed to remain "on the wing" during the entire period it is absent from its day roost. These bats fly near the ground and follow definite routes (usually along natural depressions in the topography) when dispersing from day roosts to feeding grounds, which may be several kilometers distant (Bateman and Vaughan, 1974). The average flight speed of *P. parnellii* along a natural flyway is 17.5 km/h

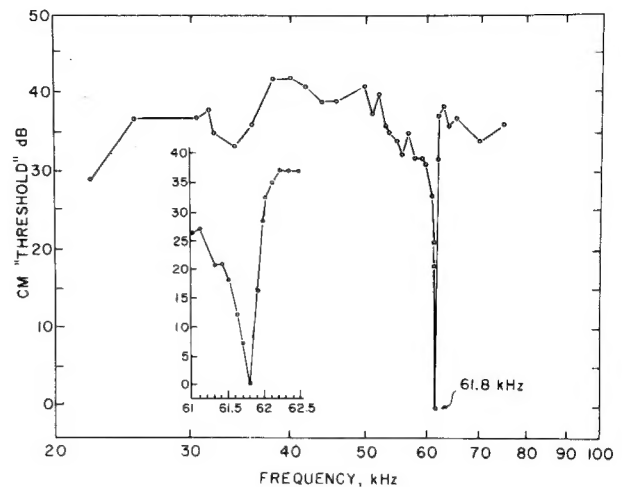


FIGURE 5. Cochlear audiograms from an awake *Pteronotus parnellii parnellii* (from Pollak et al., 1972, by permission of G. Pollak and the Amer. Assoc. Advancement Sci.). The threshold is expressed in decibels relative to the threshold at the best frequency (61.8 kHz). The insert shows the sharply tuned portion of the same audiogram in greater detail.

(Kennedy et al., 1977). Parnell's mustached bat has been variously reported to consume Lepidoptera (Bateman and Vaughan, 1974), mainly Coleoptera (Whitaker and Findley, 1980), and mainly Coleoptera and Lepidoptera (Howell and Burch, 1974). The latter authors reported that the sympatric *P. suapurensis* consumed mainly Orthoptera, suggesting food was partitioned by the two species. Selectivity in diet was supported by their rejection of lympyrid beetles, arctiid and ctenuchid moths, and the geometrid moth, *Thyrinteina arnobia*, when fed together with other prey insects in the laboratory (Goldman and Henson, 1977).

Pteronotus parnellii may be infected with several diseases hazardous to humans. Rabies has been reported in *P. parnellii* from Mexico (Villa-R. et al., 1963, fide Constantine, 1970). The average rate of infection with *Histoplasma* (which causes histoplasmosis) in Parnell's mustached bats from Central America was 25%; infection rates differed between roosts and at the same roost over a period of time (Shacklette and Hansenclever, 1969). *Scopulariopsis* (scopulariopsosis) was reported in *P. parnellii* from Colombia (Marinkelle and Grose, 1966, fide Constantine, 1970). Spinturnicid mites and bat flies (Streblidae) found on *P. parnellii* and other mormoopids differ from those of the closely related phyllostomids (Smith, 1972). The mites, *Cameroniella thomasi* and *Periglischurus elongatus*, were first described from *P. parnellii* (Furman, 1966; Machado-Allison, 1965).

In captivity *P. parnellii* may be maintained on a diet of mealworms, with a vitamin supplement being added to their drinking water. They should be kept in a cage with ample room for exercise at about 27°C and 50% relative humidity. Excess growth should be regularly trimmed from their toe nails (Rasweiler, 1977).

BEHAVIOR. The echolocation system of *P. parnellii* has received considerable attention. The echolocation calls contain a large constant frequency (CF) component, and the bat is able to detect and analyze Doppler-shifted echoes to glean information about its surroundings. Each echolocation pulse consists of three components: a brief initial upward frequency modulated (FM) sweep; a relatively long (16 to 28 msec) CF component; and a terminal 2 to 3 msec FM component (Fig. 4). The greatest amount of energy is contained in the components of the second harmonic and of these the terminal FM is typically the most intense (Pollak and Henson, 1973). The pulses are emitted orally (Griffin and Novick, 1955). The anterior longitudinal part and the posterior transverse part of the cricothyroid muscle together determine the frequency structure of the call. A second filter mechanism is present (Suthers and Durrant, 1980). During free flight *P. parnellii* emits either single sounds or groups of two sounds in synchrony with the wingbeat and respiratory cycle, with a repetition rate as fast as 8 to 12 pulses per min. Targets are first detected when a returning echo overlaps the outgoing pulse, thus a bat emitting a 20 msec pulse should be able to detect targets at 3.5 m. The one-to-one correlation between wingbeat and the emission of groups of sound is maintained as the bat approaches a target, but the bat produces more pulses per group

and reduces the intergroup interval. Pulse duration decreases as the bat closes in on the target, largely as a result of shortening of the FM component. As a consequence there is no pulse-echo overlap of FM component and the bat may process the information content of the FM portion of echoes in a manner similar to that used by other bats (Schnitzler and Henson, 1980).

The intense CF component of the call of *P. parnellii* continues to be emitted while echoes return to the ear. This pulse-echo overlap results in an echo-masking situation, which in most mammals reduces the sensitivity of the ear to sound. To overcome echo-masking the cochlea of *P. parnellii* is acoustically isolated from transcranial bone conduction of vibrations from the larynx, produced during pulse production, by being loose in the skull, and by being supported by blood sinuses, fat, and loose connective tissue (Henson, 1966). The cochlea is also sharply tuned in the 60.8 to 63.0 kHz range (Fig. 5); the intense CF component of the call is always below the sharply-tuned frequency, but with movement between bat and target, the CF component of the echo is Doppler-shifted into a more sensitive portion of the hearing range. The cochlea of *P. parnellii* shows the greatest degree of frequency specialization recorded in any mammal (Pollak et al., 1972). The middle ear muscles of *P. parnellii* contract strongly during the emission of the CF component of the pulse and relax during the terminal FM sweep (Henson and Henson, 1972). The contracted muscles achieve a marked attenuation (up to 30 dB) of frequencies up to 59 kHz, thereby protecting the ear from all components of the fundamental as well as the intense terminal FM of the second harmonic. Doppler-shifted echoes falling in the sensitive part of the audiogram are probably never so loud that protection is required, and thus may be perceived even during periods of pulse-echo overlap (Pollak and Henson, 1973).

During flight, the emission frequency (compared to that at rest) is lowered in order to compensate for the Doppler shifts caused by flight movement, thereby keeping the echo frequency constant at the sharply tuned reference frequency of the cochlea (Schnitzler, 1970, fide Gustafson and Schnitzler, 1979). Analysis of echo Doppler shift may not only be used to perceive target velocity (Schnitzler, 1973, fide Simmons, 1980); it also facilitates perception of target fluttering movements (Schnitzler, 1978, fide Simmons, 1980). Thus, Goldman and Henson (1977) observed that Parnell's mustached bats were only attracted to insects which were beating their wings.

The echolocation system of *P. parnellii* is convergent upon that of the Rhinolophidae and Hipposideridae, but they possess very different morphological specializations to achieve a high degree of frequency resolution necessary for their Doppler shift compensation type of echolocation. The cochlea of *P. parnellii* differs from that of *Rhinolophus ferrumequinum* in having a large perilymphatic duct and round window openings, a basilar membrane which remains relatively constant in width throughout most of the cochlea, a specific region which is sparsely innervated, an area where the *stria vascularis* is enlarged, dilated regions of the perilymphatic space, and a unique thick-massed haemoglobin in the scala tympani (Henson and Henson, 1980a; Pye, 1980a). The cochlea of both groups are large and reflect their specialized CF echolocation pulses (Pye 1980b). The structure of the cochlea of *P. parnellii* was described in further detail by Henson (1973, 1978, 1979), Henson and Henson (1979a, 1979b, 1980a, 1980b), Henson and Jenkins (1981), and Pye (1980b).

Small frequency modulations in the echo in the CF component are encoded in cochlear microphonic potentials (Johnson et al., 1974) and are synchronized with neural responses (Suga and Jen, 1977). The ascending auditory pathways in the brainstem of *P. parnellii* may contain a unique indirect pathway from the cochlear nucleus to the central nucleus of the inferior colliculus (Zook and Casseday, 1980). The central gray matter and the midbrain reticular formation contain neural circuits for the emission of species-specific orientation sounds (Suga et al., 1973). Representation of acoustic information from the environment in the cerebral cortex of *P. parnellii* is discussed by Suga and O'Neill (1980). To avoid being jammed by the calls of conspecifics, neurons of the auditory cortex involved in target ranging respond only to an echo after prior stimulation by the production of the corresponding pulse (O'Neill and Suga, 1980). Many of the electrophysical phenomena associated with acoustic orientation in *P. parnellii* were reviewed by Novick (1977).

GENETICS. The karyotype of *P. parnellii* is similar to that of other mormoopids: the diploid number is 38; the fundamental number is 60. The Y chromosome is subtelocentric and roughly two-thirds the size of the X chromosome; the latter is medium-sized and submetacentric. The banded pattern of the karyotype was described by Patton and Baker (1978). The electrophoretic patterns of serum proteins and haemoglobin have been used in systematic studies of this bat (Gerber and Leone, 1971; Valdivieso and Tamsitt,

1974; Valdivieso et al., 1969). The single hemoglobin has a Rf value (mobility relative to human hemoglobin A) of 0.66 (Mitchell, 1970).

REMARKS. Smith (1972) regarded the two genera, *Pteronotus* and *Mormoops*, as apparently representing a basal evolutionary dichotomy within the Mormoopidae, members of the genus *Mormoops* being more specialized than those of the genus *Pteronotus*. Within *Pteronotus*, the subgenus *Phyllodia* is more distinct from *Chilonycteris* and *Pteronotus* than are the latter subgenera from each other (Smith, 1972). The status of individuals occurring in a zone of morphological intergradation between the subspecies *P. p. mesoamericanus* and *P. p. rubiginosus* needs clarification (Smith, 1972).

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